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Micro-arthropod community responses to ecosystem retrogression in boreal forest

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ABSTRACT

Explaining the variation in communities of soil organisms across plant communities or ecosystems remains a major challenge for ecologists. Several studies have explored how soil communities are affected along ecosystem successional gradients but most of these are based on relatively short term chronosequences. To address the impact of ecosystem age on micro-arthropod communities, we utilized a 5000 year old post-fire chronosequence, which consists of thirty lake islands differing greatly in time since fire in the boreal forested zone of northern Sweden. The Acari community did not change along this chronosequence, indicating that Acari rapidly (<60 yr) reach equilibrium after forest fire and that they are relatively unresponsive to subsequent long term changes in plant community composition and soil quality. The Collembola community composition, however, showed greater responsiveness to the chronosequence and this was best explained through their functional traits. Notably, the youngest (most recently burned) islands, which had the highest ecosystem productivity and fungal mass turnover, were dominated by soil-dwelling (eu-edaphic) Collembola species that are best positioned to take advantage of resource input to the soil. Although plant community characteristics did not emerge as powerful drivers of the Collembola community, we found that Collembola community composition was related to the quality (N and P) of the soil substrate, which reflects a long term legacy of the plant community. Collembola life history characteristics proved to be important for understanding how abundances of different taxa varied relative to one another across the gradients of plant diversity and substrate quality gradients that occur across long-term chronosequences. The causal connection between vertical stratification of Collembola and substrate quality is at present unclear but is likely to be related to their feeding preferences and microhabitat conditions. Because the soil-dwelling Collembola showed a strong decline in abundance with ecosystem retrogression while surface-dwelling Collembola did not these two life history groups may operate as functionally distinct groups within the soil food web across these long-term chronosequences.

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1. Introduction

Explaining the high diversity and spatial variation of soil organisms within ecosystems and across regional scales is still a major challenge for ecologists. A large part of this challenge arises from the variation in environmental filters behind soil community

assembly that exist across space and time (Ettema and Wardle, 2002; Bardgett *et al.*, 2005). Soil quality and the presence, productivity and diversity of plants are assumed to be the major drivers behind the community composition of soil animals at local scales (Wardle *et al.*, 1999; Nielsen *et al.*, 2010, 2012; Berg, 2012), because in combination they determine habitat and resource availability. However, historical events can determine the strength of these drivers at larger regional scales (Zaitsev *et al.*, 2013). Therefore, to understand the drivers of diversity and community composition of soil animals we need to not only identify the potential environmental filters that exist at present but recognize the

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role of historic events that helped to create these environmental filters and how these may have changed across time.

Studies of ecosystem succession, such as through the use of chronosequences, often enable effective evaluation of the drivers of soil animal communities. There are a variety of reported responses of the soil animal community to successional gradients, which emerge because different successional gradients differ in various factors such as the type of vegetation present, abiotic properties and the time span of the succession (Hågvar, 1982; Hågvar and Abrahamsen, 1984; Zaitsev et al., 2002; Hågvar et al., 2009; Schrama et al., 2012; Zaitsev et al., 2013) as well as the nature of the disturbance that initiated the succession (Chauvat et al., 2011; Perez et al., 2013). Further, most studies on how soil animal communities respond to succession have focussed on their composition, species richness and diversity, while few have focused on the functional trait spectra of soil organisms, despite the insights that can be gained about community responses through the use of trait-based approaches (McGill et al., 2006; Ackerly and Cornwell, 2007; Suding et al., 2008; Messier et al., 2010). For instance, grouping micro-arthropod species according to their vertical distribution across the soil-litter profile (e.g., into epi-edaphic, hemi-edaphic and eu-edaphic life history categories) incorporates various traits related to physiological acclimation and dispersal ability (Gisin, 1943; van Dooremalen et al., 2013) and has been very successful in explaining community responses to changes in plant diversity, soil quality, moisture availability, habitat fragmentation and disturbances (Berg and Bengtsson, 2007; Krab et al., 2010; Makkonen et al., 2011; Bokhorst et al., 2012, 2013). Eu-edaphic or soil-dwelling species which feed on fungi and plant roots should be most responsive to soil quality and root exudates (Milcu et al., 2010) while hemi- and epi-edaphic species that live in the litter layer and associated plants may benefit from a greater diversity in habitat structure provided by aboveground plant parts (Sabais et al., 2011).

Our efforts to explore soil community responses along gradients of vegetation succession would benefit from utilizing long-term chronosequences that incorporate a wide range of plant diversity and soil fertility and that also include large potential shifts in functional traits of the soil community. In very long term chronosequences (i.e., where ecosystems have remained undisturbed for millennia or beyond) ecosystem succession proceeds to a state of 'ecosystem retrogression' that is characterized by increasing limitation of nutrients (notably nitrogen (N) and phosphorus (P)), impairment of decomposition processes, and reduced plant standing biomass and productivity (Walker et al., 1987; Wardle et al., 2004; Peltzer et al., 2010). Several long term chronosequences that have undergone retrogression have been identified in a range of ecosystems around the world (Walker and Syers, 1976; Vitousek et al., 1995; Parfitt et al., 2005; Selman and Hart, 2010; Laliberté et al., 2012) and these sequences show at least partly similar responses for a range of aboveground and belowground properties. Retrogressive chronosequences allow for powerful tests of how belowground communities respond to long term changes in the plant community and soil environment, without the strong legacies of human activity often present in shorter term chronosequences. A handful of studies have explored the responses of nematode communities and soil macrofauna to ecosystem retrogression (Williamson et al., 2005; Doblas-Miranda et al., 2008; Jonsson et al., 2009) but to our knowledge the response of micro-arthropod (mite and springtail) communities remains largely unexplored. This is despite their high diversity and crucial role in driving belowground ecosystem processes in many ecosystems worldwide (Filser, 2002; Wall et al., 2008).

For the present study we used a well-studied chronosequence consisting of thirty islands lacking a history of major anthropogenic disturbance in northern Sweden and spans ca. 5000 years. This

chronosequence results from the variation in fire frequency across islands with larger islands burning more frequently due to lightning strikes relative to smaller islands (Wardle and Zackrisson, 2005). This generates a chronosequence of islands differing in time since the most recent fire. As time since fire increases (and island size decreases), quality of litter inputs and litter decomposition rates diminish, leading to significant humus accumulation on the smaller islands, causing available nutrients in the soil to be locked up (Wardle et al., 2012a). In addition, there is a shift in the fungal community, with fungi that produce better protected hyphae reaching a greater abundance on the smaller islands (Clemmensen et al., 2013). Furthermore, the poorer resource quality on the smaller islands leads to reduced intensity of plant competition and greater coexistence of plant species (Wardle and Zackrisson, 2005; Wardle et al., 2008) and thus greater plant species diversity (Wardle et al., 2012a). Therefore, this island chronosequence provides a natural gradient in plant species richness, diversity and soil quality, which allows testing of the impact of these factors on the soil micro-arthropod community. We hypothesize that 1) abundances of micro-arthropods will decline with decreasing island size and as time since fire and retrogression proceeds, because of poorer quality of resources; diversity and richness of taxa will meanwhile be greater on small islands despite predictions to the contrary from island biogeography theory (MacArthur and Wilson, 1963), because of greater plant diversity and therefore habitat heterogeneity (Wardle, 2006). However, the response to island size will vary for different micro-arthropod groups and we therefore also hypothesize that 2) the community composition on the larger islands will be dominated by soil-dwelling (eu-edaphic) species due to the higher soil fertility on those islands (Hågvar, 1982) while surface-dwelling (hemi- and epi-edaphic) species will dominate the plant species-rich but less fertile smaller islands. By addressing these hypotheses we aim to provide a better insight in the driving roles of vegetation succession and ecosystem change, and concomitant shifts in plant diversity and soil quality on the community structure of soil micro-arthropods.

2. Materials and methods

The study area consisted of 30 forested islands of contrasting sizes in two neighbouring lakes in northern Sweden: Lakes Uddjaure and Hornavan (65° 55' N to 66° 09' N and 17° 43' E to 17° 55' E). All islands were formed following the retreat of land ice about 9000 years ago. The mean annual precipitation is 750 mm, and the mean temperature is 13 °C in July and −14 °C in January. The only major abiotic extrinsic factor that varies among islands is the history of lightning ignited wildfire, with larger islands having burned more frequently than smaller islands because of their larger area to intercept lightning; time since the most recent fire varies among islands from 60 to over 5000 years (Wardle et al., 1997, 2003a). Consistent with previous studies on this system (Wardle et al., 2003a; Wardle and Zackrisson, 2005; Clemmensen et al., 2013), we divided the islands into three size classes with 10 islands per class: large (>1.0 ha), medium (0.1–1.0 ha) and small (<0.1 ha), with a mean time since last major fire of 585, 2180 and 3250 years, respectively (Wardle et al., 2003a). As such, the three island size classes represent stages of early, mid and late succession respectively. On larger islands the vegetation is dominated by early successional species such as *Pinus sylvestris* and *Vaccinium myrtillus*, while late successional species such as *Picea abies* and *Empetrum hermaphroditum* dominate on small islands (Wardle et al., 1997). Previous studies on these islands have shown that as islands become smaller and time since fire increases, they enter a state of 'ecosystem retrogression' (Peltzer et al., 2010) in which there is a

Table 1

One way ANOVA statistics (F and P values) of micro-arthropod abundances, richness, diversity and community weighted mean (CWMs) life history in relation to successional stages [early, mid and late successional (i.e., retrogressive) stages, corresponding to large, medium and small islands respectively]. Values in bold are statistically significant at $P = 0.05$. For both Collembola and Acari all P -values of <0.006 remain statistically significant at $P = 0.05$ when Bonferroni corrections are applied.

	$F_{(df;2,27)}$	P
Collembola		
Total abundance	1.33	0.282
epi-edaphic species abundance	1.63	0.214
hemi-edaphic species abundance	0.51	0.607
eu-edaphic species abundance	6.75	0.004
Species diversity (H')	2.98	0.068
Species richness	3.04	0.064
CWM vertical distribution	7.44	0.003
PC1	0.26	0.773
PC2	3.40	0.048
Acari		
Total abundance	0.46	0.638
Astigmata-Prostigmata abundance	0.40	0.673
Oribatida abundance	0.65	0.531
Mesostigmata abundance	0.81	0.456
Species diversity (H')	3.80	0.035
Species richness	1.60	0.219
PC1	4.20	0.025
PC2	0.60	0.580

reduction in soil fertility (notably a reduced availability of plant-available N and P), plant biomass and ecosystem productivity, and an increase in plant species diversity (Wardle et al., 1997, 2003a). Coupled with this, the quality of litter inputs to the soil diminish, resulting in the accumulation of a thick organic layer up to a meter in depth (Wardle et al., 2003a, 2012a). Further details on the study system are given in the Supplementary Table S1.

2.1. Soil micro-arthropod community sampling

We quantified the micro-arthropod community from three separate intact soil cores, including the aboveground vegetation (10 cm diameter to a depth of 8 cm) for each of the ten islands in each of the three size classes. The O-horizon layer was deeper than 8 cm in the vast majority of cases, although some soil cores on large islands did on occasion include a very thin layer of mineral soil at the lower end of the cores. Soil percent C (and thus soil organic matter concentrations) and bulk density are consistent across the island size gradient and do not vary with island size class (Supplementary Table S1). Consistent with previous studies on these islands (e.g., Wardle et al., 2003a, 2012b), we sampled at the same distance from the shore (5–15 m) irrespective of island size to prevent confounding edge or microclimatic effects. Sample collection was done during the first two weeks of August 2011. Immediately upon collection soil cores were stored in close-fitting plastic jars (1.5 L) with an airtight lid and kept in a cooling-box during transport to storage at 5 °C and extraction. A modified Tullgren extractor (van Straalen and Rijninks, 1982) was used to extract micro-arthropods from each soil core over a three week period. Due to extraction limitations the extractions were performed in two instalments; the first instalment ($n = 36$ cores) started the same day that collection was performed while the second instalment ($n = 54$ cores) were stored for two weeks in a cold room (5 °C) before extraction. Each of the three island size classes was equally represented during both extraction sessions, eliminating the possibility of island size class-related biases.

After extraction, all Collembola were identified to species level following Fjellberg (1998, 2007) and we found 32 different species

Fig. 1. Collembola community abundance across early, mid and late successional (retrogressive) stages corresponding to large, medium and small islands respectively. a) Collembola abundance with species grouped according to their life history, i.e. whether they live in the soil (eu-edaphic), in the litter layer (hemi-edaphic) or on plants or litter (epi-edaphic). b) Community weighted mean (CWM) life history depending on adaptations to living in the soil (number of ocelli, development of furca, and level of body pigmentation). Bars are mean of $n = 10$ with SE as error bars and different letters indicate significant (Tukey HSD $P < 0.05$) differences from each other for the eu-edaphic Collembola and the CWM life history. ANOVA statistics are shown in Table 1.

across the islands. For two families (Hypogastruridae and Tullbergiidae) identification remained unresolved, but these occurred in only a few samples and very low numbers. All extracted Acari were grouped into Mesostigmata, Oribatida and Prostigmata (also including any Astigmata) following Krantz and Walter (2009). Mesostigmata were identified to family level and Oribatida were further identified to species level following Weigmann (2006). We identified 21 Oribatida species across the islands. However, five of those 21 were only identified to genus level (and were used as morphospecies) because their taxonomy has not been resolved to such a level that we can confidently identify individuals to species in this type of study. Further, for this reason, there were two additional families (Damaeioidea and Camissidae) for which further identification remained unresolved but these also occurred at low numbers when they did occur. Data from the three cores from each island were averaged so that for each variable each island was represented by a single data point, as the individual islands served as the units of replication.

2.2. Collembola community traits

To identify changes in community traits of Collembola across the island size classes we calculated community weighted mean

Fig. 2. Specific Collembola and Acari abundances across early, mid and late successional (retrogressive) stages, corresponding to large, medium and small islands respectively. Only taxa that show statistically significant differences across successional stages (one way ANOVA, $P < 0.05$) are depicted. *Isotomiella minor* and *Megalothorax minimus* are both small eu-edaphic Collembola species while *Orchesella flavescens* is a large (4 mm) epi-edaphic Collembola. Phthiracaridae are medium sized Oribatida. Bars are mean of $n = 10$ with SE as error bars and different letters indicate significant (Tukey HSD $P < 0.05$) differences between successional stages.

(CWM) trait spectra separately for each island (i.e., by pooling data from the three cores from that island), based on the approach of Fortunel et al. (2009) and Garnier et al. (2007). All Collembola species were grouped into three categories of life history that reflects their vertical distribution in soil: epi-edaphic (living on top of the soil), hemi-edaphic (living among the litter layers) and eu-edaphic (living in deeper soil layers), as these categories incorporate a large suite of traits related to thermal acclimation, mobility and association with the different soil-litter layers (Gisin, 1943; Berg et al., 1998; van Dooremalen et al., 2013). Eu-edaphic, hemi-edaphic and epi-edaphic species were given a trait score of 1, 2 and 3, respectively. For each island, the relative abundance of each Collembola species present was multiplied with its trait value, and this was summed for all the species present on that island to provide the CWM life history. Low CWM values indicate a dominance of soil-dwelling species and represent adaptations to deeper soil conditions while high values indicate a dominance of surface-living species and represent adaptations to living in the litter layer and on plants. Assignment of all Collembola species to the three categories is given in Table 1. Information on vertical distribution of Acari families was unavailable so this analysis was limited to the Collembola only.

2.3. Calculations and statistical analyses

For each island, Shannon diversity index (H') was separately calculated for Collembola species and Oribatida species. Principal Component Analyses (PCA) was used to summarize the microarthropod community data for Collembola species and Oribatida species into fewer variables. One-way ANOVA (with individual

islands serving as independent replicates) was used to test for the effect of island size class (three levels, i.e. small, medium or large) on all response variables including total abundances of taxa, CWM life history, measures of taxonomic richness and diversity, and scores for the two principal axes derived from PCA. In addition, correlation analysis (with each island serving as an independent data point) was used to relate these variables to island size, time since fire, soil N, P, N:P, plant species richness, plant diversity (H') and plant biomass, using previously published data from these islands presented by (Wardle et al., 2003a, 2012b, 2004; Lagerström et al., 2009). Homogeneity of variance was tested using Levene's test of equality and log transformation was applied when necessary. All statistical analyses were done using SPSS 20.0 (SPSS Inc., Chicago, Ill., USA).

3. Results

3.1. Collembola community composition across islands

Three of the nine variables relating to Collembola were significantly related to successional stage (i.e., island size class) at $P = 0.05$, as opposed to the 0.45 variables that would be expected by chance (Table 1). Total Collembola abundance did not differ across the three successional stages (i.e., island size classes), but abundance of eu-edaphic Collembola did (Table 1), as eu-edaphic Collembola were more than twice as abundant in the earliest successional stage than in oldest successional or retrogressive stages (Fig. 1a). This difference among successional stages was reflected by species-specific abundances of typical eu-edaphic species, such as *Isotomiella minor* and *Megalothorax minimus*, which had their

Table 2

Pearson's correlation coefficients (r) of micro-arthropod community variables with island size, time since fire, nutrients (N and P) and plant species richness (R) and plant diversity (H'). Decreasing island size is a proxy for successional time with smaller islands representing a retrogressive stage. Correlations are based on n = 30 islands. *P < 0.05, **P < 0.01, ***P < 0.001. CWM: Community weighted mean trait; PC: Principal Component axis scores. For each row all r-values of >0.45 or < -0.45 remain statistically significant at P = 0.05 when Bonferroni corrections are applied.

	Island size	Time since fire	Soil N (%)	P (%)	N:P	pH	Plant R	Plant H'	Plant Biomass
Collembola									
Total abundance	0.194	-0.144	-0.230	-0.034	-0.148	0.395*	-0.077	-0.139	0.395*
Epi-edaphic species abundance	-0.079	0.018	0.177	0.004	0.132	0.085	0.235	-0.077	0.149
Hemi-edaphic species abundance	0.124	-0.017	-0.151	-0.133	-0.018	0.344	-0.095	-0.142	0.293
Eu-edaphic species abundance	0.435*	-0.403*	-0.506**	0.220	-0.530**	0.394*	-0.281	-0.113	0.365*
Species richness	0.437*	-0.348	-0.373*	0.112	-0.356	0.394*	-0.162	-0.203	0.405*
Diversity (H')	0.330	-0.487**	-0.447*	0.104	-0.416*	0.370*	-0.144	-0.109	0.161
CWM	-0.381*	0.372*	0.550**	-0.171	0.515**	-0.310	0.325	0.058	0.395*
PC1	-0.207	-0.081	0.008	0.052	-0.038	-0.220	0.099	0.142	0.149
PC2	0.191	-0.184	-0.463**	0.157	-0.434*	0.449*	-0.203	0.044	0.293
Acari									
Total abundance	0.181	0.059	0.142	0.139	0.061	0.263	-0.032	-0.08	0.197
Astigmata-Prostigmata abundance	0.327	-0.133	0.086	0.052	0.059	0.102	-0.192	-0.292	0.243
Oribatida abundance	0.049	0.154	0.124	0.172	0.030	0.286	0.057	0.042	0.222
Mesostigmata abundance	0.279	-0.118	-0.097	0.127	-0.109	0.448*	-0.116	-0.092	0.166
Species richness	-0.044	0.008	0.144	-0.230	0.165	0.000	0.078	0.000	0.015
Diversity (H')	-0.13	0.05	0.044	0.004	0.145	-0.088	0.102	-0.035	0.086
PC1	0.105	-0.02	-0.036	0.000	-0.087	0.134	-0.063	0.005	-0.125
PC2	-0.025	0.032	0.071	0.001	0.050	-0.038	0.162	0.050	0.024

highest abundances at the earliest successional stages (Fig. 2a and b, Supplementary Table S2). While total abundance of hemi- and epi-edaphic species was independent of successional stage (Fig. 1a), the epi-edaphic springtail *Orchesella flavescens* was most abundant in the earliest successional stage (Fig. 2c, Supplementary Table S2). The CWM life history was significantly lower, at the earlier successional stage than at the older stages, indicative of a greater dominance of soil-dwelling species at the earlier successional stage (Fig. 1b).

Collembola species diversity (H') and species richness were almost significantly related to successional stage at $P = 0.05$. Both measures were highest on the earliest successional stage; for diversity (H') values (mean $\pm$ SE) were 2.0 ± 0.0 , 1.8 ± 0.1 and 1.9 ± 0.1 on early, mid and old stages, respectively, while for species richness corresponding values were 14.3 ± 0.5 , 11.9 ± 0.7 and 11.5 ± 1.2 , respectively. These successional stage differences in species richness were mainly driven by the richness of epi-edaphic species which differed among stages (ANOVA: $F_{2,27} = 3.9$, $P < 0.033$), with 5.2 ± 0.4 , 4.1 ± 0.4 and 3.5 ± 0.6 species on early, mid and old stages, respectively. These species richness differences were influenced in part by *Dicyrtomina minuta*, *Entomobrya multifasciata* and *Lipothrix lubbocki* which were present in the early and mid stages but not in the latest successional or retrogressive stages (Supplementary Table S2). There was no effect of successional stage on PC1 scores, but there was for PC2 scores (Table 1), with *I. minor* and *M. minimus* having a strong association with the early stages (Supplementary Fig. S1).

For the correlation analysis of Collembola variables with environmental variables, 24 of the 81 relationships were significant at $P = 0.05$, as opposed to the 4 variables that would be expected by chance (Table 2). Total Collembola abundance was positively correlated with plant biomass and soil pH (Table 2). Epi- and hemi-edaphic species abundance was not correlated with any of the main soil and plant characteristics across the successional stages. Eu-edaphic Collembola abundance was positively correlated with island size, plant biomass, soil pH and negatively with time since fire, N content and N:P ratio. Species richness was positively correlated with island size, soil pH and plant biomass but negatively with soil N content. Species diversity (H') was negatively correlated with

time since fire, N content and N:P ratio, but positively with soil pH. The CWM life history was negatively correlated with island size but positively with time since fire, N content, N:P ratio and plant biomass. The PC1 scores for the Collembola community were unrelated to any successional characteristic, while PC2 scores were negatively correlated with soil N content and N:P ratio. There were few significant correlations of individual Collembola species with island characteristics (Supplementary Table S3). Among these was the epi-edaphic species *Lepidocyrtus lignorum* which was negatively correlated with island size and soil P content but positively with soil N:P ratio. Further, the most abundant eu-edaphic species *I. minor* and *M. minimus* were negatively correlated with soil N content and N:P ratio and *M. minimus* was positively correlated with plant biomass.

3.2. Acari community composition across islands

Two of the nine variables relating to Acari were significantly related to chronosequence stage (i.e., island size class) at $P = 0.05$, as opposed to the 0.45 variables that would be expected by chance (Table 1). There were no differences across the three chronosequence stages in abundances of total Acari, any of the major groups or Oribatida richness (Table 1). Oribatida diversity (H') was lowest at the mid stage (1.07 ± 0.07) and highest at the late successional or retrogressive stage (1.46 ± 0.15) with the earlier successional stage having intermediate values (1.15 ± 0.08) ($F_{2,27} = 3.8$, $P < 0.05$). The ordination scores along PC1 were lowest for the late successional stages while the mid stage had highest values ($F_{2,27} = 4.2$, $P < 0.05$; Supplementary Fig. S1) but there were no differences for PC2. The abundance of the Oribatid *Phthiracarus anonymus* was lowest in the early successional stages (Fig. 2d), and *Edwardzetes edwardsi* and *Pergalumna nervosa* only occurred in the late successional or retrogressive stages (Supplementary Table S4). The abundance of the Oribatid mite *Eulohmannia ribagai* was negatively correlated with plant diversity, while *Phthiracarus anonymus* was negatively correlated with island size and positively with time since fire and soil N:P (Supplementary Table S3).

4. Discussion

Against the predictions of the first hypothesis, total numbers of Collembola and Acari did not decline as retrogression proceeded, and community diversity and species richness did not increase. Instead, the Collembola community patterns across succession stages (i.e., island size classes) were better explained by community traits as revealed by the CWM life history values, in support of our second hypothesis. Typical community metrics such as diversity (H') and species richness were poor predictors of the micro-arthropod community across this chronosequence, indicating the need for a stronger focus on species traits (Violle et al., 2007; Fortunel et al., 2009; de Bello et al., 2011; Perez et al., 2013).

In addition to the relatively few relationships of the abundance of micro-arthropods with chronosequence stage, there were no significant correlations between micro-arthropod diversity (H') or richness and island size. Plant species richness and diversity increase as island size decreases, which should serve to increase the diversity and heterogeneity of the litter that serves as the main habitat for many micro-arthropod species (Wolters, 1987; Salamon et al., 2004; Krab et al., 2013). The failure of abundance, diversity or richness of Collembola and Acari to show any relationship with plant richness and diversity is contrary to what has often been observed in various grassland communities (Wardle et al., 1999, 2003b; Salamon et al., 2004; St John et al., 2006; Sabais et al., 2011) and across some vegetation gradients with high species turnover (Perez et al., 2013). It is possible that the differences that exist between the islands in plant community structure (Wardle et al., 1997) and plant trait spectra (Wardle et al., 2012a) are not large enough to impact on measures of micro-arthropod abundance or diversity (Bokhorst et al., 2014). Alternatively, as the ecosystems being compared are islands of varying size, island biogeography theory would predict a higher number of species or diversity on larger islands (MacArthur and Wilson, 1963). However, as plant (and therefore, presumably microhabitat) diversity declines as island size increases, it is possible that biogeographical effects of island size and effects of plant diversity have opposing effects on Collembola diversity across the gradient, resulting in little or no net-response to the gradient. Furthermore, diversity and richness metrics ignore the individual characteristics of species and therefore any potential associated community differences based on relative species abundances that exist between the islands.

In support of our second hypothesis we found a lower CWM life history for Collembola in the early successional stages, which is indicative of a community that has a greater contribution of soil-dwelling (eu-edaphic) species, and this is consistent with the greater abundances of eu-edaphic species observed in the early successional stages. The reduced fire frequency in the oldest successional stages has been shown to lead to reduced soil fertility, and a poorer quality of litter inputs to the soil, which would be expected to disproportionately impair soil dwelling species. Further, it has been shown that as ecosystem retrogression proceeds in this system, there is a shift in domination of the fungal community by species that produce labile hyphae (notably cord-forming Basidiomycetes) towards domination by those that produce recalcitrant, defended hyphae (notably ericoid-mycorrhizal Ascomycetes) (Clemmensen et al., 2013, 2015). This decline in fungal resource quality would be expected to impact especially negatively on fungal feeding eu-edaphic species (Ponge, 1991; Fujii and Takeda, 2012). Further work is needed to determine if the change towards more recalcitrant mycelia with ecosystem retrogression (Clemmensen et al., 2013, 2015) is primarily driven by the change in the quality of the resources produced by the plants or due to the shift in community composition of fungal-feeding Collembola and decline in fungal-feeding eu-edaphic taxa in the oldest successional stages.

Overall, the aggregation of species into life history (i.e. vertical distribution) groups (McGill et al., 2006; Leps et al., 2011) improved our ability to identify patterns of micro-arthropods across vegetation change and helped to explain these patterns.

There were no differences in measures of Acari abundance or diversity across the successional stages, suggesting that above-ground and belowground changes associated with ecosystem retrogression did not have a large impact on this group. There were however some species-specific differences across the successional stages. The Oribatid species *Phthiracarus anonymus* had higher abundance in the older successional stages, indicating that this species thrives best in the older nutrient limited soils. The Phthiracaridae are commonly recognized as pine needle litter feeders (van der Drift, 1951; Pande and Berthet, 1973), yet their abundance was greatest in the older successional stages where the contribution of pine species to the vegetation is least (Wardle et al., 2003a). This suggests that either the feeding preferences are broader than assumed (Siepel and De Ruiter-Dijkman, 1993; Maraun et al., 1998, 2003; 2011), or that preferences for specific fungal species (Koukol et al., 2009) play a role in the distribution of these mites across this chronosequence. Further, all our study islands last burned at least 60 (and up to 5000) years ago, and Oribatid abundance has typically been found to reach equilibrium after approximately 70 years of succession in other ecosystems (Zaitsev et al., 2006; Hågvar et al., 2009). This suggests that the development of the Oribatid community may take place over shorter time periods than those represented in our study. The results indicate that the Acari community is not particularly responsive to ecosystem retrogression. However, identification of Acari to functional groups (in the manner that we performed for the Collembola) could potentially reveal stronger responses as well as a better understanding of the feeding preferences.

The current findings were the result of a one-off sampling event, and as for all studies of this type, the community composition of the soil micro-arthropods results that we observed will be reflective of climatic conditions at and prior to the time of sampling. However, it is apparent from data on the monthly precipitation, temperature and snow conditions over the 18 months during and prior to the sampling period at our study site (data obtained from the Swedish Meteorological and Hydrological Institute www.smhi.se) that the climate at and prior to the time of our sampling did not show any strong deviations from long term mean conditions, meaning that the results obtained during our sampling are unlikely to be anomalous or in any way reflective of unusual climatic conditions.

5. Conclusions

The studied island chronosequence includes strong gradients in plant diversity, composition and biomass (Wardle et al., 2012a), but these variables did not drive large corresponding changes in the micro-arthropod community. This is at variance with some studies that show microarthropod communities to be highly responsive to vegetation change in other ecosystem types (Wardle et al., 1999; van der Putten et al., 2001), suggesting that micro-arthropod communities may be somewhat decoupled from changes in the plant community that occur during ecosystem retrogression in boreal forest. However, some responses of Collembola to retrogression were detected when species were aggregated into functional groups according to their life history. In particular, shifts in soil fertility and the quality of plant litter inputs and fungal residues as retrogression proceeded was likely an important driver of abundances of soil-dwelling eu-edaphic Collembola. As such, the Collembola community consists of distinct functional groups that are characterized by their vertical stratification across the soil profile in the soil food web, each of which show distinct responses

to these boreal forest long-term chronosequences. More broadly, the use of distinct functional categories for some groups of soil organisms such as Collembola may be an important first step for understanding what drives the community composition and diversity of these groups over time and space, including among contrasting ecosystems.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.soilbio.2017.03.009>.

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